CALCIFIED *PLECTONEMA* (BLUE-GREEN ALGAE), A RECENT EXAMPLE OF *GIRVANELLA* FROM ALDABRA ATOLL

by ROBERT RIDING

ABSTRACT. *Girvanella*, not previously reported from rocks younger than Cretaceous, is described from the Recent. It occurs as the calcified sheath of the filamentous blue-green alga *Plectonema gloeophilum* Borzi in small freshwater pools on Aldabra Atoll in the Indian Ocean. The sheaths are heavily impregnated during the life of the alga by micrite grade crystals of magnesian calcite which make them hard and potentially fossilizable and which preserve the filaments as small calcareous tubes 4-10 μm in diameter. This confirms the view that *Girvanella* represents a filamentous blue-green alga preserved by the calcification of its sheath, and it extends the range of the genus from Cambrian to Recent. The consistent relatively thin-walled morphology of *Girvanella*-type impregnated sheaths contrasts with the thickly microsparite encrusted sheaths of blue-green algae in environments of $CaCO_3$ cementation. This suggests a greater degree of control of the calcification process in *Girvanella* and supports the concept of specificity for calcification in some blue-greens. *P. gloeophilum* is believed to be only one of a number of extant filamentous blue-greens whose calcified sheaths are referable to *Girvanella*. At present *Girvanella* is still most conveniently placed in the Porostromata, which should be regarded as a group of tubiform calcareous algae.

THE size and morphology of the microscopic tubiform fossil *Girvanella* Nicholson and Etheridge suggest that it is the calcified sheath of a filamentous blue-green alga (Pollock 1918; Riding 1972, 1975). Blue-greens are among the oldest known fossils and the similarities between very ancient and extant forms indicate that they are morphologically conservative organisms (Schopf 1968, p. 653). If *Girvanella* is indeed a blue-green alga then it is reasonable to expect that it has a modern representative. Yet although *Girvanella* is known to range from the Cambrian to Cretaceous it has not previously been recorded from the Cenozoic (Riding 1975). The purpose of this paper is to draw attention to a Recent example of *Girvanella* from the Indian Ocean atoll of Aldabra.

This living *Girvanella* is the small filamentous blue-green alga *Plectonema gloeophilum* Borzi. It inhabits freshwater pools on Aldabra and its sheath in these habitats sometimes becomes heavily impregnated during life by $CaCO_3$ which renders it hard and potentially fossilizable. The resulting simple sinuous calcareous tube is a small form of *Girvanella*. It seems likely that a variety of filamentous blue-greens from several families can, under suitable conditions, produce calcareous tubes referable to *Girvanella* or to related fossil genera. Thus, *P. gloeophilum* is thought to be only one of a number of extant blue-greens whose soft parts show them to be quite distinct taxa, but whose simple calcified sheaths can be bracketed together in the single fossil genus *Girvanella*.

CALCIFIED BLUE-GREEN ALGAE

Cyanophytes have a long geological record as calcified and silicified fossils and as algal stromatolites. Stromatolites are organosedimentary structures; they do not

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readily reflect the types of organisms involved in their construction, which may include coccoid and filamentous bacteria and blue-green algae and also green algae. By contrast silicified fossil blue-greens can show remarkable preservation of the soft tissue, including details of cellular ultrastructure. Thus, stromatolitic and silicified blue-green algae represent extremes of preservation. They also differ markedly in abundance, stromatolites being relatively common whereas silicified microfloras are rather rare.

Calcified blue-green algae are intermediate between stromatolitic and silicified forms in the degree of morphological detail which they retain, and probably also in their over-all abundance through geological time. In the discussion of calcification (see below) it will be necessary to distinguish between calcification of the sheath on the one hand and massive encrustation of the filament on the other, both being types of calcification. But in *Plectonema* and *Girvanella* we are only dealing with the former. Calcification in this case only affects the mucilaginous sheath enclosing the strands of cells (trichomes). It takes place while the alga is living. Because $CaCO_3$ is incorporated into the sheath rather than into the cell walls of the alga only the external morphology of the algal filament is preserved and most of the features which are significant for the taxonomy of Recent blue-greens are lost (text-fig. 1). Filamentous
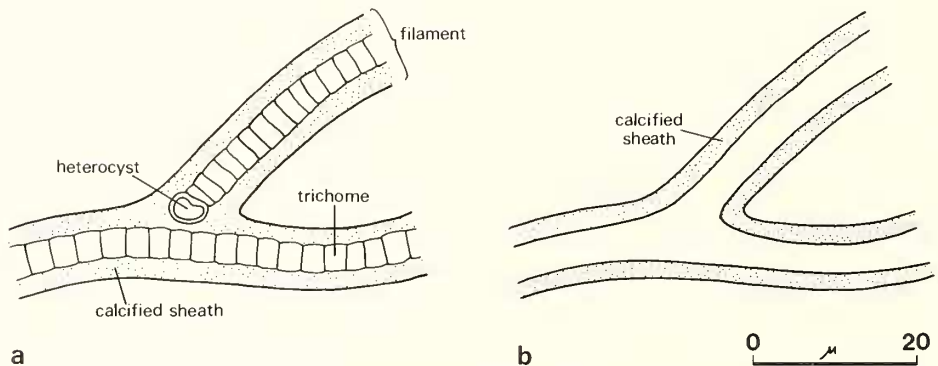

TEXT-FIG. 1. Post-mortem loss of morphological detail in calcified filamentous blue-green algae. The alga shown is *Tolypothrix*, a scytonematacean similar to *Plectonema* but possessing heterocysts. *a*, portion of living calcified filament. *b*, empty, potentially fossilizable, calcified sheath. Features observable in *a* but not in *b* include: presence of heterocyst, type of branching (false), number (one) and size of trichomes. The sections are longitudinal.

blue-green algae calcified in this way produce microscopic, morphologically simple, non-septate tubiform skeletons which may exhibit branching but which show few other distinctive characters. The relatively large diameters of these calcareous tubes and their lack of septa clearly distinguish them from the rather small trichomes of blue-green algae which are strands of cells. The expectation by some previous workers that fossil calcified blue-greens should reflect the form of the trichomes, and so be very small and septate, has tended to hinder recognition of the cyanophyte origin of the larger, non-septate calcified sheaths.

Nevertheless, Pia (1927, pp. 37-40) realized the true affinities of several of these small fossils but, being unable to relate them directly to Recent blue-green taxa, he

erected the group Porostromata to contain them. Not all of the genera originally included by Pia in the Porostromata appear to be blue-greens, but two of them, *Girvanella* and *Ortonella* Garwood (text-fig. 2), are regarded here as definitely having this affinity. Johnson's (1961, pp. 96-99) removal of several porostromate genera to the green Codiales was unwarranted (Riding 1975) and has subsequently confused the identity of fossil calcified filamentous blue-green algae. Much earlier Pollock (1918) had already made the suggestion, which is confirmed here, that *Girvanella* is a calcified cyanophyte sheath.
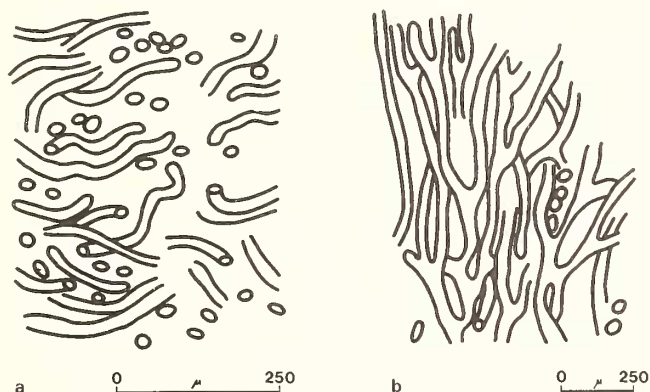
TEXT-FIG. 2. Morphology and orientation of *a*, *Girvanella*, and *b*, *Ortonella*, from photomicrographs of the type-specimens in Nicholson and Etheridge 1878, pl. 9, fig. 24; and Garwood 1914, pl. 20, fig. 2. *Girvanella* is flexuous, prostrate, and generally unbranched. *Ortonella* is straight, erect, and dichotomously branched. These contrasting features were used by Pia (1927) to separate the Porostromata into the Agathidia and Thamnidia respectively.

While it is unlikely that fossil calcified blue-greens can be referred to *single* extant genera it should be possible to discern closer relationships between fossil and living forms than are expressed by current palaeontological classifications and hence to improve our understanding of the nature and environmental significance of fossil calcified blue-green algae. I have suggested that the existence of Recent *Girvanella* is to be expected (Riding 1972) and that representatives are most likely to be found among filamentous blue-green families such as the Oscillatoriaceae, Rivulariaceae, Scytonemataceae, and Stigonemataceae (Riding 1975). The small Recent scyto-nematacean *P. gloeophilum* provides one such example of living *Girvanella*.

CALCIFIED *PLECTONEMA* FROM ALDABRA

Habitat. *P. gloeophilum* occurs in small freshwater pools on West Island, Aldabra; an atoll in the western Indian Ocean, 1200 km WSW. of the Seychelles. Aldabra receives an annual rainfall of approximately 1000 mm (D. R. Stoddart, pers. comm.). The freshwater pools, classed as 'temporary rainwater rockholes' by McKenzie (1971) are mostly very small, with volumes usually less than 3 m³. Their water chemistry and algal flora have been studied by Donaldson and Whitton (1976*a*, *b*). The pools provide water for tortoises, birds, crabs, and other animals and tend to become contaminated by excreta which produce

high concentrations of phosphate and ammonia. There is locally also some sea-water contamination of the pools, but they are essentially fresh. The pools support a varied algal flora with filamentous blue-greens such as *Calothrix, Oscillatoria, Phormidium*, and *Plectonema* usually present (Donaldson and Whitton 1976*b*). The locations of Aldabran pools are described by Donaldson and Whitton (unpublished).

The specimens of *Plectonema* described here were collected by Alan Donaldson from adjacent pools W7 and W127 on West Island (text-fig. 3) and he has kindly supplied the following details of their occurrence. These pools have volumes of approximately 1·8 and 0·3 m³ respectively. *Plectonema* forms mats on
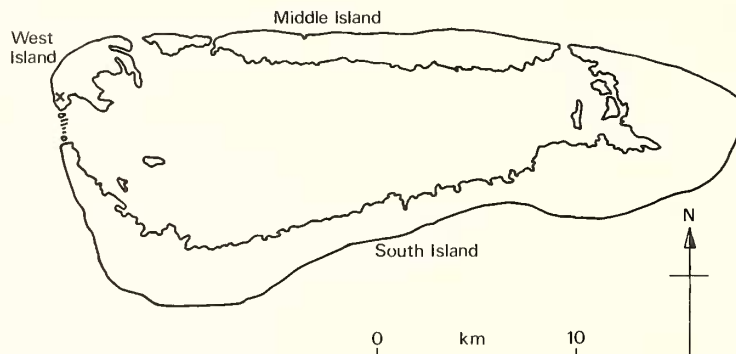
TEXT-FIG. 3. Location (**X**) of adjacent *Plectonema*-containing pools W7 and W127 on West Island, Aldabra.

lime mud and silt flooring the pools. Collection of gas bubbles within the mats lifts them from the sediment and they rise to the surface to form dense globular flocs approximately 1 cm in diameter which are pale pink in colour and heavily calcified. In pool W7 from January to June 1973 *Plectonema* was associated with a wide variety of unicellular and filamentous green and blue-green algae. The following parameters of the pool-water were recorded by Donaldson during this period:

mean Ca concentration: 72·1 mgl⁻¹
mean Mg concentration: 18·8 mgl⁻¹
pH: 7·5–8·6
temperature: 25·3–36·7 °C.

No measurements were made of pool W127 situated some 50 m north of pool W7. In April 1973 pool W127 contained a virtual uniculture of *P. gloeophilium* with abundant calcified flocs, samples of which are described and illustrated here.

Methods. The samples of *Plectonema* were air-dried in the shade following collection. For atomic absorption spectrophotometry small specimens were dissolved in 20% HCl. The insoluble residue constituted less than 5% by weight of the specimen. Mineralogy was determined by X-ray diffractometry. For scanning electron microscopy specimens were fractured and coated with carbon and gold. The photographs were taken on a Cambridge Stereoscan Mark II instrument operating at 20 kV.

Description. *P. gloeophilum* is a small, filamentous blue-green which shows false-branching and is non-heterocystous. The sheath is generally thin and contains a single trichome. The entire filament is 4–10 μm in diameter, and the sheath is up to 3 μm in thickness. Calcified sheaths of this species from pool W127 are figured in Plate 11. They form dense tangled masses of sinuous macaroni-like tubes. The CaCO₃ occurs as bladed and acicular micrite crystals 1–3 μm in size which form tufted clusters crudely orientated normal to the surface of the filament giving it a test-tube brush appearance. These crystals are calcite containing 4·6 mole % MgCO₃ and thus are close to the 4 mole % division between low- and high-magnesian calcite. Traces of the sheaths occur as patches and strands on the surfaces of the calcified tubes in the SEM. Biological preparations of the material show the calcite crystals to be contained within or very close to the surface of the sheath. Drying of the sheath in air, and in vacuum during preparation for electron

microscopy, causes it to shrink and exposes the crystals which then form very irregular inner and outer surfaces to the tube. The calcified tubes are approximately 6 μm in external diameter and 2 μm in the thickness of their walls. They exceed 140 μm in length and do not taper.

Comparison with Girvanella. *Girvanella* is a small, flexuous, rarely branching, tubi-form fossil with a microgranular (micritic) calcareous wall (text-fig. 4). Specimens
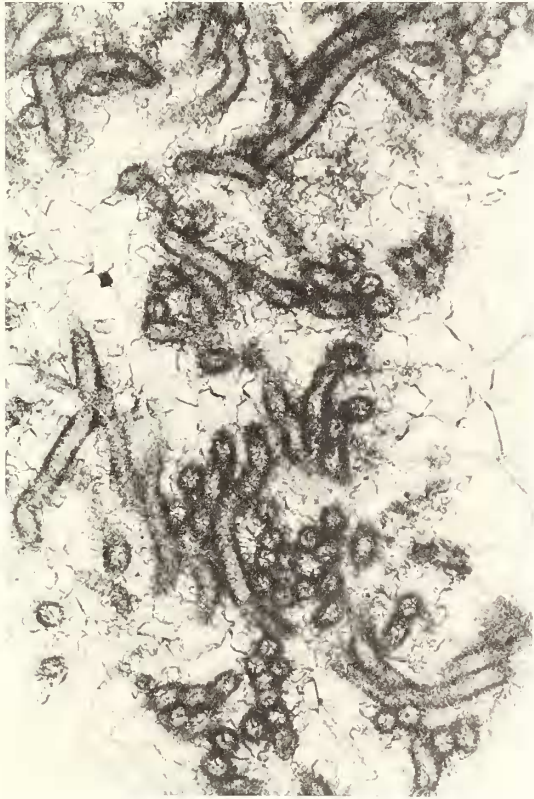
TEXT-FIG. 4. *Girvanella* sp., from the Upper Devonian (Frasnian), Mount Hawk Formation, Mount Haultain, Alberta. Note constancy of tube diameter and relatively thin wall. Thin section courtesy of E. W. Mountjoy (McGill University); $\times$ 125.

with external tube diameters from 1 to 100 μm are recorded in the literature. Whether the larger sizes really represent *Girvanella* is open to question but certainly the genus exhibits a large size range. Most specimens recorded have diameters in the range 8–30 μm. For each specimen the tube diameter is constant and the total wall thickness is approximately 50% of the external diameter. *Girvanella* occurs encrusting grains or as small discrete masses which are themselves grains. Whether the latter are fragments or are original unbroken masses of filaments is not usually clear.

The similarity between *Girvanella* and the calcified *Plectonema* sheaths described here is striking. The ratio of wall thickness to tube diameter in *Plectonema* (2:3)

somewhat exceeds that in *Girvanella* (approximately 1 : 2) and the surface of the tube is more irregular, but it is likely that both these features would be reduced during diagenesis. Otherwise there are no observable differences between *Girvanella* and these specimens of *Plectonema*.

OTHER CALCIFIED ALGAL FILAMENTS

Although this is the first specific report of Recent *Girvanella*, calcified algal filaments have previously been noted in several studies of Recent intertidal and supratidal algal mats from the Bahamas. Black (1933, p. 170, pl. 22, fig. 28) first noted that the supratidal algal mats of the interior of Andros Island tend to be calcified. Monty (1967, p. B67, pl. 6) compared calcified filaments of *Scytonema myochrous* from the supratidal of eastern Andros with *Ortonella*. These specimens of *Scytonema* are erect and dichotomously branched and are approximately 20 μm in external diameter. Calcified *Scytonema* filaments have also been figured from the supratidal of north-western Andros by Shinn *et al.* (1969, fig. 12*b*) but these specimens are less upright in appearance and resemble *Girvanella* more than *Ortonella*. Similar tubules have been described from calcareous crusts in late Pleistocene limestones of Barbados (James 1972, fig. 6*d*). They are 15–20 μm in external diameter with a wall thickness of approximately 5 μm and are composed mainly of equant calcite crystals 1·5–2·5 μm in size (James 1972, p. 826). James compared them with filaments of the extant blue-green alga *Schizothrix* and attributed them to 'blue-green algae or possibly root-hairs'. They closely resemble the calcified *Plectonema* sheaths from Aldabra in morphology, but they are larger.

Calcite encrusted cyanophyte filaments which are rather different from those described here have been reported from freshwater stream tufa in south-western Germany (Irion and Müller 1968). The filaments belong to Recent oscillatoriacean blue-greens 'with a diameter of 5 μm; they are encrusted by isometric crystals with a rounded surface. The average diameter of the crystals is 15 μm' (Irion and Müller 1968, p. 165). Apparently the crystals form a thick crust *on*, rather than *within*, the sheath. The specimens are not figured but it can be inferred that they would be tubes with diameters of at least 35 μm. Their thick walls (more than 85% of the tube diameter) and microsparite grade crystals distinguish them from *Girvanella* and *Plectonema* tubes.


EXPLANATION OF PLATE 11

Scanning electron micrographs of calcified sheaths of *Plectonema gloeophilum* Borzi from freshwater pool W7, West Island, Aldabra.

Fig. 1. Tangled 'ball of knitting wool' appearance of mass of tubes, × 220.

Fig. 2. Detail of Fig. 1 showing unbranched, uniform diameter sheaths associated with thin dried strands of mucilage. Large uncalcified filament in the upper part of the photograph is probably the green alga *Oedogonium*, × 1100.

Fig. 3. Surface of calcified filament showing bladed and acicular micrite grade crystals of magnesian calcite. Note general orientation of crystals normal to sheath surface, and traces of dried mucilage, × 5500.

Fig. 4. Fracture (or termination) of filament showing relatively thin wall and hollow interior, × 5400.

PLATE 11
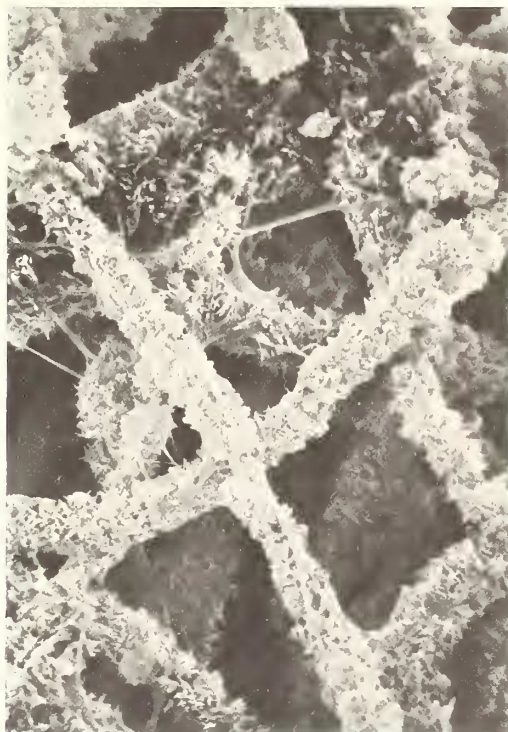

RIDING, calcified *Plectonema*

There are relatively few records of Recent calcified blue-green filaments from subtidal marine environments. Winland and Matthews (1974, fig. 3c) figure calcified sheath material associated with grapestone from Great Bahama Bank. The form of the filament is not shown but it has a diameter of 10–12 μm and a sheath thickness of approximately 2 μm. The $CaCO_3$ crystals are 1–2 μm in size and have rhombic and acicular forms. These sizes and shapes are similar to those of the crystals in *Plectonema* from Aldabra. A circular structure, which may be a cross-section of a similar filament, has been figured from Recent Red Sea reefs (Friedman *et al.* 1974, fig. 15), although it could also be a pellet. It is 9 μm in diameter with a wall thickness of 3 μm and consists of high-magnesian calcite. Calcified filaments of the green alga *Ostreobium* have been described from Recent Bermudan cup reefs (Schroeder 1972). This endolithic alga has a diameter of 2–20 μm. The principal morphological difference between *Ostreobium* and blue-green algal filaments is the local swellings shown by the green alga. *Ostreobium* is not normally calcified but in small internal cavities in the cup reefs it has become encrusted by equant, bladed, or fibrous crystals of high-magnesian calcite during early subsea cementation. The calcite crystals also encrust adjacent non-algal surfaces. The crystals are relatively large with widths of 5 μm and lengths of 10–20 μm being common. Not only are the *Ostreobium* filaments externally encrusted but, following decay of the alga, the remaining cavity is also infilled by calcite crystals. Hence the filaments are preserved by thick external crusts plus internal cores. The core is up to 20 μm in diameter and the crust is up to 150 μm in thickness (Schroeder 1972, p. 20). Thus, the total diameter of the calcified filament ranges from 15 to 300 μm or more, and it is ultimately preserved as a rod rather than as a tube. Heavily encrusted filaments of this type resemble those of blue-green algae from freshwater streams and tufa deposits.

D. R. Kobluk and M. J. Risk inform me that they have seen calcification of *Ostreobium* filaments projecting from experimentally introduced Iceland spar crystals in a shallow subtidal environment at Jamaica. Micrite and microspar low-magnesian calcite crystals coat the inner and outer surfaces of exposed dead filaments and give rise to thickly encrusted rods 8–30 μm in diameter comparable with those described by Schroeder.

DISCUSSION

There are two distinct types of calcified blue-green algal filament: micrite-*impregnated* sheaths and microspar-*encrusted* sheaths (text-fig. 5). Calcified Aldabran *Plectonema*, and by analogy fossil *Girvanella*, represent impregnated sheaths without significant external encrustation. The Bahaman filaments described above from both the supratidal (Black 1933; Monty 1967; Shinn *et al.* 1969) and subtidal (Winland and Matthews 1974) fall within the same category. In contrast blue-green filaments in freshwater tufa (Irion and Müller 1968) are thickly encrusted, as are subtidal cemented green algal filaments (Schroeder 1972).

Any heavily encrusted filaments recorded as fossils should be distinguishable from *Girvanella* and *Ortonella* tubes in being wider, having greater wall thickness, being composed of coarser crystals, showing variability in diameter within a single specimen, and in some cases by being infilled by additional cement to form a rod. These
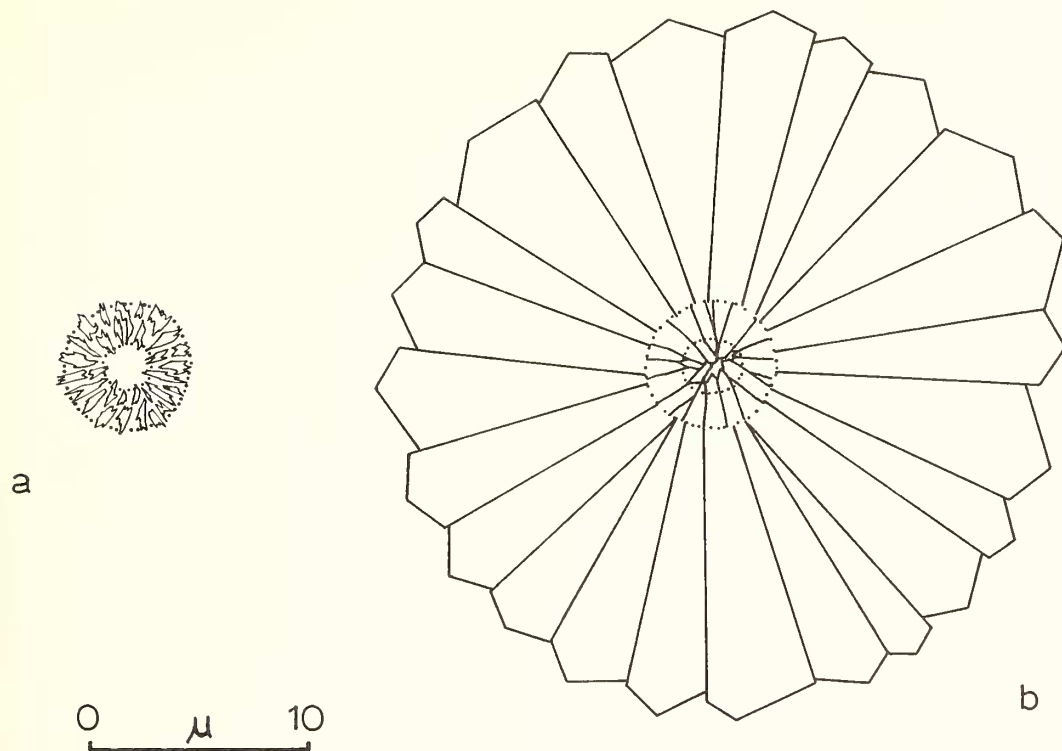
TEXT-FIG. 5. *a*, micrite impregnated, and *b*, microspar encrusted sheaths in diagrammatic cross-section. The consistent thin-walled morphology of *Girvanella* (type *a* sheath) throughout its geological history indicates that *a* and *b* do not simply represent different stages of the same process but that different mechanisms of calcification are involved: 'controlled' (essentially biochemical) in *a*, 'uncontrolled' (essentially physicochemical) in *b*.

contrasts between thickly encrusted sheaths and impregnated sheaths suggest that at least the *rate* of the calcification process is operating differently in the two cases, but there is also circumstantial evidence which suggests that the *type* of process differs as well.

Calcification. It has gradually become clear that calcification processes operate quite differently in different algal groups (see Arnott and Pautard 1970) and are to some extent reflected by the site of $CaCO_3$ deposition on or within the plant. In the red Corallinaceae the site of calcification is the cell wall; in the green Codiales and Dasycladales it is mainly extracellular but the calcareous skeleton forms an intimate part of the plant body. In Aldabran *Plectonema*, and apparently in calcified blue-greens generally, calcification is entirely extracellular, being restricted to the mucilaginous external sheath. This suggests a mechanism which is not entirely under the control of the plant's metabolism and is supported by the variable occurrence of calcification in the group since no blue-green species is known to be always calcified. It is tempting to go on to hypothesize an essentially physicochemical precipitation mechanism in calcified blue-greens, even though this is not applicable

to any other calcareous algae, and two supporting lines of evidence can be derived from Aldabran *Plectonema*.

(i) *Environment of occurrence*. $CaCO_3$ precipitation due to photosynthetic utilization of CO_2 will be limited in normal marine environments by the buffering capacity of sea-water, but this regulation will not operate in fresh water where removal of CO_2 species can readily cause precipitation. The relatively high temperature, pH, and calcium concentration of the Aldabran pools containing calcified *Plectonema* are conditions favouring $CaCO_3$ precipitation and removal of CO_2 from the system during algal photosynthesis could provide the final stimulus for this process.

(ii) *Nature of the* $CaCO_3$. Three features of the *Plectonema* skeletons described here are 1, calcite mineralogy; 2, micrite-grade crystal size; and 3, incorporation of magnesium. Calcite formation is inhibited in sea-water by abundance of magnesium cations but it is the normal phase to be precipitated in fresh water. The Mg content of the calcite indicated by the AAS analyses is probably an over-estimate because it will include magnesium from the organic sheath material (see Gebelein and Hoffman 1971) due to the acid preparation method used. Even so it is only low in the high-magnesian calcite range and can be seen as a reflection of the magnesium content of the pool-water. The small size of the calcite crystals is probably due to a rapid crystallization rate. Thus, the mineralogy, composition, and texture of the $CaCO_3$ in these algal sheaths are consistent with their meteoric, surficial environment of formation (see Folk 1974, fig. 5). This conformity with normal physicochemical controls of carbonate mineral formation is another indication that biological involvement in the precipitation process could be limited.

There are, however, two significant features of blue-green calcification which raise doubts about a simple physicochemical mechanism.

(i) Calcification in blue-greens is variable but it does not appear to be wholly controlled by the environment since certain species seem to be more predisposed to calcification than others. This specificity for $CaCO_3$ deposition is suggested by studies reported by Golubić (1973, p. 436) and is supported by the mutual occurrence of calcified and uncalcified blue-green species.

(ii) If *Girvanella* were primarily dependent upon cementation processes for its skeletogenesis then its wall thickness could be expected to vary greatly according to the degree of precipitation proceeding in the micro-environment of a particular specimen. It should be capable of greatly exceeding the 50% of the tube diameter characteristic of the genus. Furthermore its tubiform morphology should be modified, in some cases at least, by infilling by a cement core as in *Ostreobium* reported by Schroeder and others. Yet thick microsparite-walled *Girvanella*-type fossils and similar rod-shaped forms are conspicuous by their absence from the geological record of the past 600 ma. This morphological discontinuity between *Plectonema/Girvanella* tubes (impregnated sheaths) and encrusted sheaths suggests that the former are produced by blue-green algae which have the capacity to control calcification and are not simply dependent upon an external physicochemical process.

Accordingly it is reasonable to postulate a distinction not only between the degree of calcification, i.e. between impregnated and encrusted sheaths, but also a corresponding distinction in the control (and timing) of calcification, i.e. between essentially *controlled* and *uncontrolled* calcification in blue-green algae. In forms such as

Girvanella and *Ortonella* and their Recent analogues I suggest that the alga exerts a controlling influence over calcification and promotes crystal deposition in the sheath but not beyond it. The skeleton is thus a relatively thin-walled tube formed during the life of the alga. In other calcified forms known from freshwater tufa deposits and from Recent environments of subsea cementation calcification is beyond (or extends beyond) the control of the plant and results in gratuitous deposition of $CaCO_3$ either during life or post-mortem. These skeletons are relatively thick-walled tubes or rods.

Thus, while several features of $CaCO_3$ deposition in blue-greens are consistent with an essentially physicochemical control photosynthetically triggered by an otherwise passive alga, the morphology of *Girvanella* and its Recent analogues together with the mutual occurrence of calcified and uncalcified forms support the concept of specificity for, and control of, calcification in some blue-greens. The degree of control is clearly not complete since a species which calcifies in one habitat will not necessarily calcify elsewhere. Yet it is of interest that even the relatively unsophisticated blue-greens could have a control over their calcification which might be as distinctive, if less refined, as those operating in green, yellow-green, and red algae. But the nature of this calcification mechanism in blue-greens has still to be elucidated.

Taxonomic significance. The specimens of *Plectonema* from Aldabra and those of *Scytonema* described by Monty (1967) provide Recent analogues of *Girvanella* and *Ortonella* respectively. Is *Girvanella* really *Plectonema*, or the other way round? The answer is neither. The amount of morphological detail preserved by *Girvanella* and *Ortonella* is so limited (text-fig. 1) that it could relate to a wide variety of extant filamentous blue-greens (Riding 1975). It is likely that both *Girvanella* and *Ortonella* represent a number of Recent biological taxa, of which *Plectonema* and *Scytonema* are only two. Thus, *Plectonema* is represented by the entire alga, trichomes as well as sheath. But its calcified sheath when the soft parts have been removed is *Girvanella*. *Girvanella*, on the other hand, is a calcified blue-green algal sheath devoid of soft parts. It is only distinguished from other calcified sheaths by its generally unbranched, sinuous morphology, constant diameter, and prostrate habit. In contrast, *Ortonella* is erect with subparallel filaments and dichotomously branched (text-fig. 2).

This distinction between *Girvanella* and *Ortonella* is very crude when compared with the probable multiplicity of biological taxa merged within them, but it is possible that some environmental information can be gleaned from their gross differences in external morphology to compensate somewhat for the loss of detail in soft-part structure. Rather than merely representing a variety of taxa they might represent groups of morphologically similar ecophenes (environmental growth forms) of a variety of taxa. The distinction between erect and prostrate form seen in *Ortonella* and *Girvanella* extends to a number of porostromate genera and was recognized by Pia (1927, pp. 37–40) when he subdivided the Porostromata into the Agathidia (prostrate forms such as *Girvanella* and *Sphaerocodium*) and Thamnidia (erect forms such as *Hedströmia*, *Mitcheldeania*, and *Ortonella*). The erect, tufted habit of the Thamnidia suggests phototropic growth possibly induced by physical confinement, while the prostrate habit of the Agathidia suggests higher

light availability. But caution should be exercised in these interpretations and a genetic, as opposed to environmental, control of these forms cannot be excluded (B. A. Whitton, pers. comm.).

Pia intended the Porostromata to contain calcareous tubiform fossils which he believed to be blue-green algae but which he was unable to place in extant groups. In practice the affinities of genera normally included in the Porostromata have been in doubt and attempts to use the group as a 'Section' of the Schizophyta (bacteria and blue-green algae) have not been very successful (see Johnson 1961, p. 194). Instead the Porostromata have been most useful not as a group of fossil calcareous blue-green algae but as a group of small tubiform fossils. In my view this is still the case and will remain so until the affinities of more members of the group can be clarified. It would be premature to assume that because there is now good evidence that two genera, *Girvanella* and *Ortonella*, are the calcified sheaths of filamentous blue-greens that this confirms Pia's view of the group as a whole. It is still possible that calcified green algae are represented by some of the porostromate genera, especially those with relatively large tubes, and an apparent transition from Porostromata with closely appressed tubes to members of the Solenoporaceae remains to be clarified. Neither would it be advantageous at present to remove *Girvanella* and *Ortonella* from the Porostromata and place them in extant blue-green families because of the probability that they represent forms from several families. The members of the Porostromata form a reasonably homogeneous morphological group characterized by their microscopic, calcareous, non-septate, tubiform skeletons. It should be retained as a group of algae rather than blue-green algae. The following genera can be included: *Bevocastria* Garwood, *Cayeuxia* Frollo, *Girvanella*, *Hedströmia* Rothpletz, *Mitcheldeania* Wethered/*Garwoodia* Wood, *Ortonella*, *Sphaerocodium* Rothpletz. *Epiphyton* Bornemann, originally included by Pia, is not tubiform, and *Ottonosia* Twenhofel and *Somphospongia* Beede, included in the group by Johnson (1961, pp. 195–196) are aggregates of porostromate tubes, not tubiform fossils themselves.

CONCLUSIONS

1. Calcified *P. gloeophilum* in freshwater pools on Aldabra is a Recent analogue of *Girvanella*. It is a 'living fossil' in the sense that *Girvanella*, while known to range from Cambrian to Cretaceous, was previously unrecorded from Cenozoic rocks. This discovery confirms previous suggestions that *Girvanella* represents the calcified sheaths of filamentous blue-green algae (Pollock 1918; Riding 1972, 1975) rather than being a calcified green alga (Frémy and Dangeard 1935; Johnson 1963, p. 26).

2. In fresh water and marine environments where $CaCO_3$ cementation is common, small algal filaments can become thickly encrusted by microspar. Limitation of calcification to the sheath in *Plectonema* and *Girvanella* produces a quite different, consistently thin-walled, tubiform micritic skeleton suggesting that precipitation of the crystals does not proceed uncontrolled in this case. This supports the idea that certain blue-greens have a specific capacity for calcification. However, the fact that *Plectonema* is not *always* calcified indicates that control of calcification by the alga

is partial, rather than complete, and is presumably dependent on some overriding environmental factors.

3. The morphological discontinuity between calcified sheaths and encrusted filaments, together with differences in their environment of occurrence, support a distinction between relatively controlled and relatively uncontrolled calcification in blue-greens. Controlled calcification can proceed in a variety of carbonate environments, not only those where cementation and tufa-formation are general, and occurs in living algae. Micrite crystals impregnate the sheath but do not significantly encrust its external surface. In this way the size and form of the sheath are preserved. Uncontrolled calcification only takes place in environments of cementation and tufa-formation and can occur during life or post-mortem. Filaments are encrusted by microspar or larger crystals to form a thick-walled tube which only grossly reflects the original morphology of the alga. The interior of the tube may be infilled to produce a solid rod of $CaCO_3$. Controlled and uncontrolled calcification seem to reflect contrasting mechanisms of $CaCO_3$ deposition, the former essentially biochemical, the latter essentially physicochemical.

4. *Girvanella* probably includes various filamentous blue-green algae and not solely fossil *Plectonema*. Consequently, the Porostromata remains the most suitable higher taxon in which *Girvanella* can be placed at present. The Porostromata includes some blue-green genera, but also others whose precise affinities remain uncertain. It should be regarded as primarily a morphological group of algae.

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R. RIDING

Department of Geology
University College
Cardiff CF1 1XL